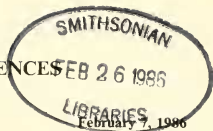


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**ACANTHOGILIA, A NEW GENUS OF POLEMONIACEAE
FROM BAJA CALIFORNIA, MEXICO**

By

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ABSTRACT: We propose the genus *Acanthogilia* for the spiny desert shrub first named *Gilia gloriosa* Brandege. The gametic chromosome number is nine, also the basic number for nine other genera and for the family.

Acanthogilia is unique among Polemoniaceae in its extreme leaf dimorphism, its persistent woody-spinose primary leaves, and its coarsely verrucate zonocolporate pollen grains. Though formerly placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, it differs further from all these genera in its persistent secondary leaf bases with deciduous blades, its numerous closely spaced corolla veins connected at several levels, and its winged seeds. It does share several unusual characters, such as the superficially adnate filaments, with species of *Gilia* sect. *Giliastrum*.

Acanthogilia seems closest to the Andean genus *Cantua*. *Cantua*, like *Acanthogilia*, is shrubby, with leaves dimorphic, on long shoots and axillary short shoots, with persistent leaf bases, with corolla veins connected at several levels, with winged seeds, with superficially adnate filaments (in some species), and with coarsely verrucate pollen grains (in one other species). *Cantua* differs in having the leaves broad and herbaceous, only weakly dimorphic, and neither woody-spinose nor with deciduous linear blades, the calyx entirely herbaceous, the pollen pantoporate, and the chromosome number hexaploid.

INTRODUCTION

Gilia gloriosa, of T. S. Brandege (1889), is a spiny but truly gloriose desert shrub of rather local occurrence on the Pacific drainage of north-central Baja California (Fig. 1-3). This plant is seldom seen and little known, and its best generic position has remained uncertain. Brand (1907) placed it in *Gilia* sect. *Leptodactylon*, and Wherry (1945) called it *Leptodactylon gloriosum*. Johnston (1924) informally listed it as *Loeselia gloriosa*. Current floras (Wiggins 1964, 1980) treat it as *Ipomopsis gloriosa*, following Alva Grant (in V. Grant 1956).

New information on the chromosome number, pollen grain type, and some other aspects shows that *Gilia gloriosa* differs from all de-

scribed genera of the family and has some unique characters. We therefore propose for it the following new monotypic genus.

SYSTEMATIC TREATMENT

Acanthogilia Day et Moran, genus novum mexicanum Polemoniacearum, ob folia valde dimorpha, primariis rigide spinosis persistentibus, granaque pollinis zonocolporata supraverrucata bene distinctum; Cantuae Juss. fortasse proximum, quae autem calyce toto herbaceo, aetate non rumpenti, pollinis granis pantoporatis, chromosomatunque numero polyploideo differt. Si vis descriptionem latine recipere, involucrum praeinscriptum praesolutumque mitte.

Stiff spiny shrub with dimorphic leaves, the



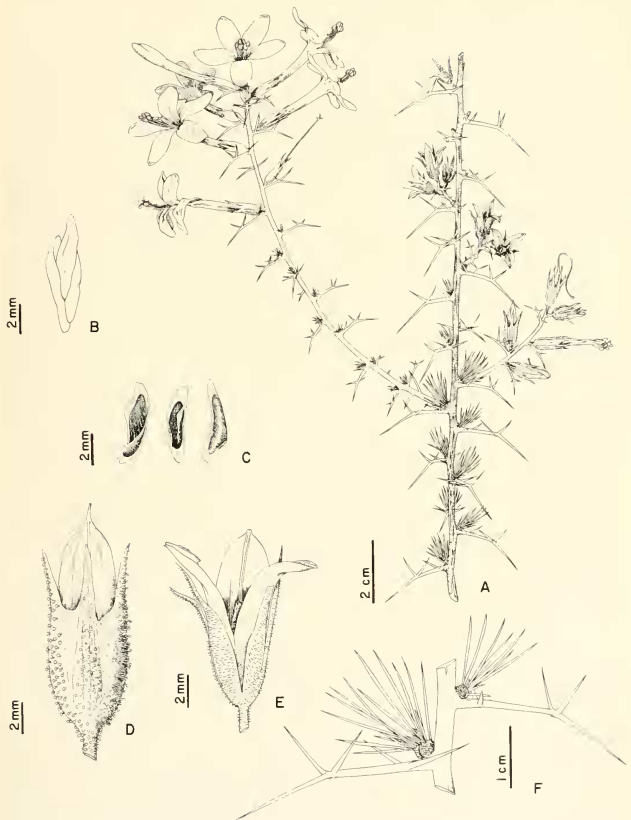


FIGURE 2. *Acanthogilia gloriosa* in flower and fruit. A. Flowering and fruiting branches on an older branch, with dehiscent capsules from previous season; B. Green, submature seeds, contents of a single locule; C. Dry seeds from dehiscent capsule; D. Calyx with mature, undeveloped capsule; E. Calyx with dehiscent capsule from previous season; F. Segment of branch with spinose primary leaves and fascicled herbaceous secondary leaves.

FIGURE 1. Inflorescence of *Acanthogilia gloriosa* (Brand.) Day and Moran, El Colosal, Baja California, Mexico, 13 June 1976.

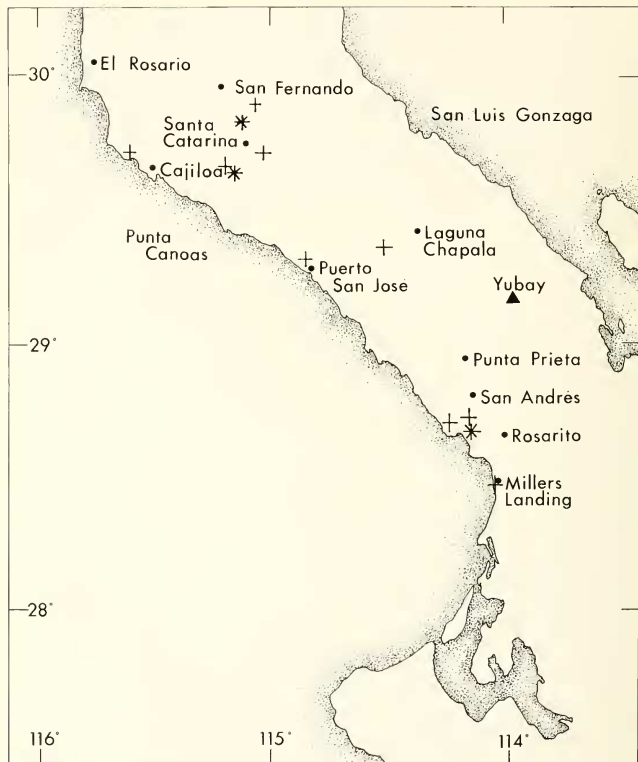


FIGURE 3. North-central Baja California, Mexico, showing distribution of *Acanthogilia gloriosa*. + = collection site, * = site of collection yielding chromosome count, \blacktriangle = stated type locality.

primary alternate, woody-persistent, pinnate, with terete spinose divisions, the secondary fascicled on axillary short shoots, with persistent bases and deciduous, flat, linear, herbaceous blades. Calyx tubular, with equal spinose lobes and narrower scarious intervals that rupture in

fruit. Corolla regular, salverform. Stamens subequally attached near middle of tube, superficially adnate below, subequal, well exerted. Pollen yellow, the grains zonocolporate, perreticulate, supraverrucate. Seeds elongate, flat, winged, mucilaginous when wet. Chromosomes: $x = 9$.

TYPE-SPECIES. — *Gilia gloriosa* Brandegee.

***Acanthogilia gloriosa* (Brandegee)**

Day and Moran, comb. nov.

Gilia gloriosa Brandegee, Proc. Calif. Acad. Sci. Ser. 2, 2:184, pl. 9. 1889. *Loeselia gloriosa* I. M. Johnston, Proc. Calif. Acad. Sci. Ser. 4, 12:962. 1924. *Leptodactylon gloriosum* Wherry, Am. Midl. Naturalist 34:383. 1945. *Ipomopsis gloriosa* A. Grant in V. Grant, Aliso 3:357. 1956.

TYPE. — Mexico, Baja California, Ubi, 8 May 1889, T. S. Brandegee s.n. (holotype, UC 101896; isotypes, DSI, GH). The type locality, Ubi, is the tinaja, or waterhole, of Yubay, near 29°11'N, 113°59'W, elevation ca. 650 m, ca. 9 km NE of the abandoned mine of Desengaño and ca. 52 km from the Pacific coast. Brandegee remarked that the plant appeared to be very local, having been observed only during an hour's journey and not again met with. He customarily gave bare locality names without direction or distance, and presumably he may have meant within half a day or so north or south of Yubay. His itinerary (Moran 1952) suggests south. Moran failed to find the plant about Yubay or along the old trail just to the south.

Stiff spiny shrub 1–3 m high and 1–5 m wide, much branched at base, the young parts glandular-pubescent and glutinous with two–many-celled trichomes mostly less than 0.5 mm long, each tipped with yellowish globule. Trunks to 6 cm thick, the bark light to dark gray, flaking in small plates; lower branches arching, sometimes rooting. Branching sympodial, the branches mostly flowering terminally the first year and so not elongating further, 1–125 cm long, 1–4 mm thick the first year, tan becoming gray, subterete, persistently spiny with old leaves; internodes averaging 5–8 mm, exceeded by leaves. Primary leaves subopposite to mostly alternate, 1–3 cm long, woody-spinose, rigidly divaricate and straight except terminal segment usually declined, green becoming tan and finally dark gray, persisting two to three (sometimes to six) years but weak after first or second year, the lowermost sometimes simple but most pinnate with narrowly linear rachis and one to two (sometimes to three) pairs of spreading spinose lobes to 9 mm long, the base 1.5–3.0 mm wide. Secondary leaves fasciated in axils, few and short the first season (on flowering branches), later to 25 per season, the bases whitish to tan, persistent, the blades herbaceous, mostly simple, rarely with one to two short lobes, linear-oblancoate, spine-tipped, flattened, 5–20 mm long, to 1 mm wide, rather sparsely glandular, deciduous throughout plant all at about one time; first leaves of new shoot with enlarged semiglobular bases to 1.5 mm wide and blades sometimes less than 1 mm long. Short shoots producing leaves for

three to four (sometimes to six) years, to 8 mm long or some becoming long shoots. Inflorescence densely glandular-puberulent and glutinous, a thyse to 2 dm long on a new shoot, with terminal flower mostly opening first and with up to 30 short one–few-flowered branches below; or inflorescence reduced to short one–few-flowered shoot, though sometimes several such shoots borne on one older branch to form two-generational inflorescence. Flowers January to July, October, protandrous, open ca. four to five days and nights, odorless, visited by hummingbirds. Pedicels erect to spreading, 1–6 mm long, 0.5–1.0 mm thick. Calyx 10–16 mm long, 3.0–4.5 mm wide, cylindric, tapering to rounded at base, densely glandular and glutinous without, more sparsely so within, tubular in lower $\frac{2}{3}$; segments equal, erect or slightly outcurved, 3–8 mm long, triangular-lanceolate, pungent-acuminate, cartilaginous, with many crowded veins within, scarious-margined except near apex; sinuses V-shaped, the scarious intervals much narrower than ribs, distended at anthesis, folding inward as segments later converge, mostly rupturing in fruit. Corolla salverform, 3.0–4.5 cm long, glandular without, in bud pale yellow becoming orange; tube stout, slightly upcurved, 2.0–3.2 cm long, 2.5–3.5 mm wide below, gradually flaring to orifice 5–7 mm wide, dull orange-red to orange-brown, becoming paler and more purplish; throat yellow; limb 2–4 cm wide, white and mucilopapillose inside, rose-veined outside, the lobes in bud convolute, in anthesis widespread or somewhat reflexed, in age strongly reflexed, 8–20 mm long, 4–12 mm wide, obliquely oval to strap-shaped, obtuse to slightly emarginate, sometimes apiculate, with 30–50 close-spaced parallel veins per lobe. Filaments glabrous, 15–27 mm long, subequally attached at middle of tube or slightly above, superficially adnate below, with margins free throughout, subequally exerted 4–13 mm from throat; anthers oblong, sagittate, 4–5 mm long before anthesis, dehiscing as corolla begins to open. Pollen grains suboblate to spheroidal (P 55–64 μ m, E 61–71 μ m). Nectary disk green, ca. 2 mm wide, shallowly cupped, the margin regularly undulate to form erect lobules opposite calyx segments and spreading ones between. Ovary three-celled, 4–5 mm long, ca. 1.5 mm thick; style 20–40 mm long, slightly shorter to slightly longer than filaments (consistent in each plant); stigma lobes acute, 1.5–2.0 mm long,

outcurved by third day. Ovules 14–24 per cell, ovoid, ca. 0.6 mm long, many aborting. Capsules 7–15 mm long, 4–5 mm thick, cylindric, beaked, crustaceous, yellowish brown, loculicidally dehiscent, the valves often recurving. Seeds overlapping, one to six per cell, narrowly oblong, flat, 6–7 mm long, 1.5 mm wide, the brownish body surrounded by elongated membranous wing, the body and wing swelling and mucilaginous when wet. Chromosomes: $n = 9$.

DISTRIBUTION.—Mexico, Baja California Norte: locally common on desert flats and hill-sides and in arroyo beds from 40 km SSE of El Rosario to Miller's Landing, a span of 200 km, and from the coast inland at least 45 km and to 525 m elevation (Fig. 3).

ADDITIONAL SPECIMENS EXAMINED.—San Fernando, 24 May 1894, *Anthony s.n.* (UC); Rosalia Bay, Jul.–Oct. 1896, *Anthony* 92 (DS, UC); 2 km NW of Cajillo, 29°41'N, 115°34½'W, Aug. 1980, *Binney s.n.* (SD); 2.9 m E of mouth of Arroyo San José, 29°12'N, 114°44'W, 28 Jun. 1969, *Bostic s.n.* (SD); 6.2 m S of Santa Catarina, 29°38'N, 115°10'W, 26 Aug. 1969, *Bostic s.n.* (SD); San Andreas Canyon above Santa Rosalillita, 20 Mar. 1984, *Breedlove* 60808 (CAS); 2–3 km NE of Santa Rosalillita, 20 Mar. 1984, *Breedlove* 60834 (CAS); 5–15 m N of Puerto Santa Catarina, road to San Agustín, 1 Mar. 1985, *Breedlove* 62269 (CAS); 1 m NE of Rancho Santa Catarina, 20 Jun. 1979, *Clark* 3167 (CAS); 10 m S of Punta Prieta, 9 Feb. 1947, *Constance* 3125 (DS); 2 km W of La Ramona, 29°49'N, 115°07'W, 10 Jul. 1976, *Day and Moran* 76-126 (CAS, SD); same data, *Day and Moran* 76-129 (CAS, SD); 4.3 m S of El Colosal, 29°47'N, 115°06'W, 10 Jul. 1976, *Day and Moran* 76-133 (CAS); Sierra Lino, 25 m S of Punta Prieta, 6 Mar. 1947, *Gentry* 7345 (DS, UC); S of Arroyo San Borja, 26 Mar. 1947, *Gentry* 7617 (DS, UC); San Andreas, 26 Jul. 1941, *Harbison s.n.* (SD); Arroyo San José, 29°10'N, 114°45'W, 18 Oct. 1966, *Hastings and Turner* 66-154 (DS, SD); Rancho La Ramona, Santa Catarina, 21 Jun. 1947, *Huey s.n.* (SD); 3 m S of Miller's Landing, 9 Jul. 1937, *Lindsay s.n.* (DS); Arroyo Santo Dominguito, 6.7 m S of San Andres, 28°42'N, 114°15'W, 28 May 1959, *Moran* 7498 (DS, SD, UC); ½ m N of Rancho Ramona, 29°50'N, 115°05'W, 25 Mar. 1970, *Moran* 16896 (SD); 11 m N of Puerto Santa Catarina, 29°39'N, 115°12'W, 28 Mar. 1970, *Moran* 17030 (SD); 3 m SE of Santa Rosalillita, 28°40'N, 114°13'W, 2 Jan. 1976 and ex hort. San Diego, 16 Jul. 1976, *Moran* 22779, (CAS, SD); 10 km S of El Águila, 29°52½'N, 115°04½'W, 12 Jun. 1976, *Moran* 23518 (SD); 2 km W of La Ramona, 29°49'N, 115°07'W, 12 Jun. 1976, *Moran* 23519 (SD); 2 km W of La Luciana Mine, 29°42'N, 115°02'W, 13 Jun. 1976, *Moran* 23521 (CAS, SD); 3 km NW of Santa Catarina, 29°44½'N, 115°06½'W, 13 Jun. 1976, *Moran* 23522 (CAS, SD); coastal region near Rosarito, 28°38'N, 114°05'W, 5 Oct. 1970, *Rauh* 25416 (HEID, SD); 1 m NW of Santa Catarina, 29°44'N, 115°06'W, *Robinson s.n.* (SD); 23 m S of Punta Prieta, 1 Jun. 1931, *Wiggins* 5731 (DS UC); 17 m S of Punta Prieta, 9 Apr. 1961, *Wiggins* 16193, (DS).

At Rancho Santa Catarina this plant was called "mala mujer" (bad woman). That name is used in Baja California and elsewhere in Mexico for

some other prickly plants, as well as for several stinging and poisonous plants (Martínez 1937).

FLORAL BIOLOGY.—Floral characters of *Acanthogilia* predominantly suggest outcrossing. The anthers dehisce as the flower opens, but stigmas do not open out until the third day. Styles usually exceed stamens, as in many Polemoniaceae that are insect- or hummingbird-pollinated. In some individuals, however, styles are consistently shorter, with stigmas opening just beneath the anthers, as in various autogamous flowers. This heteromorphism in the population may help ensure some seed production even if outcrossing fails. The floral characters strongly suggest adaptation to hummingbird pollination, and Moran has observed hummingbirds visiting the flowers. The flowers are open by day, odorless, with stamens and style well exerted. The corolla is robust, with a long and ample tube. Its color pattern is well marked, with glistening white lobes around a yellow orifice, and with an orange-red to orange-brown tube. Other hummingbird flowers in the family have similar characters. In *Cantua*, *Gilia*, *Ipomopsis*, *Loeselia*, and *Polemonium*, hummingbird flowers are diurnal and odorless, with long red or yellow corolla tubes and usually with exerted stamens and style (Grant and Grant 1965). Superficially, some hummingbird flowers of different genera look more like each other than like bee- or fly-pollinated flowers of their own genus.

COMPARISONS WITH OTHER POLEMONIACEAE

CHROMOSOME NUMBER.—The basic chromosome number of *Acanthogilia* is nine. We base it on counts from propionic-carmines squashes of anthers from three collections of *A. gloriosa* (mapped in Fig. 3): (1) *Moran* 17030 from 18 km N of Puerto Santa Catarina; (2) *Moran* 22779, ex hort. San Diego, from 4.8 km SE of Santa Rosalillita; and (3) *Moran* 23519, from 2 km W of La Ramona. Meiotic counts from collection 1 showed $n = 9$; chromosome behavior was regular, with 9_{II} at M_I (Fig. 4). From premeiotic sporogenous cells of collection 2 (Fig. 4) and from tapetal cells of collection 3, mitotic counts showed $2n = 18$.

Nine is the basic number for more than half the genera of the family (Table 1) and is regarded as the primitive basic number in the Polemoniaceae. The other genera have lower basic numbers apparently derived independently in different tribes by aneuploid reduction (Grant 1959).

Thus, *Acanthogilia* stands among the ten genera that still have the primitive number. These are a mixed lot, from all five tribes in the classification of Grant (1959). Hence chromosome number gives no clue to the tribal placement of *Acanthogilia*.

The basic number is mostly constant within genera of the family (Table 1); where it is not (*Allophyllum*, *Gilia*), the number varies by only one chromosome pair ($x = 9, 8$). *Gilia gloriosa* was placed in *Ipomopsis* (A. Grant in V. Grant 1956) before its chromosome number was known. Since *Ipomopsis* has $x = 7$, a count of $n = 9$ for *I. gloriosa* showed us it was in the wrong genus. That was the starting point for this study.

POLLEN.—Pollen studies in the Polemoniaceae (Erdtman 1952; Stuchlik 1967; Taylor and Levin 1975) have not included *Acanthogilia*. We sent a pollen sample to Dr. Leon Stuchlik, who kindly prepared the following diagnosis, in 1980, with permission to include it here (see Fig. 5–8).

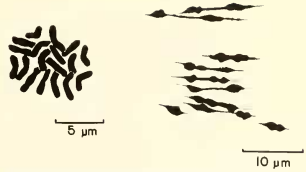


FIGURE 4. Chromosomes of *Acanthogilia gloriosa*. Left, mitosis; right, meiosis. Traced from micrographs.

Pollen grains 5–6 colpiate (zonocolporate), suboblate to spheroidal; diameter 55–64 $\mu\text{m} \times 61\text{--}71 \mu\text{m}$. Colpi short, only slightly longer than pores are broad. Pores along to circular; diameter 5–7 $\mu\text{m} \times 7\text{--}10 \mu\text{m}$. Exine 2.4–2.9 μm thick; nexine 0.8–1.2 μm thick, thickened up to 1.7 μm in pore area, finely perreticulate. Lumina variable in shape and size; diameter less than 0.5 μm to 1 μm ; muri supported by simple bacula densely spaced,

TABLE 1. COMPARISON OF THE GENERA OF POLEMONIACEAE. I, 9, 8 = intrageneric aneuploidy; 9/8 and 8/7 = dibasic polyploidy. II. Pollen groups 1–4 are the alliances of Taylor and Levin (1975), with *Acanthogilia* added. III. Pin = leaves pinnately veined, dissected, or lobed; PinC = leaves pinnately compound; Palm = leaves palmately lobed; * = true foliage leaves lacking. IV. N = seeds not winged; NW = seeds very narrowly winged; W = seeds broadly winged. V. A = filaments superficially adnate; M = filaments merged with corolla; I = filaments intermediate; merged below. VI. M = calyx membranous below sinuses; H = calyx herbaceous throughout. VII. A = veins connected at base of lobe and in upper lobe; B = veins connected only at base; C = veins connected only well above base; D = veins free; * = venation too simplified to classify.

	I Basic chromosome number	II Pollen group	III Leaf form	IV Seed type	V Filaments	VI Calyx type	VII Venation of corolla lobe
<i>Acanthogilia</i>	9	1	Pin	W	A	M	A
<i>Cantua</i>	9	1	Pin	W	A, M	H	A, B
	($2n = 27_n$)						
<i>Huthia</i>	?	1	Pin	W	I	H	B
<i>Cobaea</i>	9/8	2	PinC	W	A	H	A
	($2n = 26_n$)						
<i>Phlox</i>	7	2	Pin	N	M	M	A, B
<i>Microsteris</i>	7	2	Pin	N	M	M	*
<i>Gymnosteris</i>	6	2	*	N	M	H	*
<i>Polemonium</i>	9	3	PinC	N	M, I	H	A, B
<i>Bonplandia</i>	8/7?	3	Pin	N, NW	M	H	A
	($2n = 15_n$)†						
<i>Gilia</i>	9, 8	4	Pin	N	A, M, I	M	A, B, D
<i>Collomia</i>	8	4	Pin	N	M	H	B, C
<i>Eriastrum</i>	7	4	Pin	N	M, I	M	B
<i>Navarretia</i>	9	4	Pin	N	M	M	B, *
<i>Ipomopsis</i>	7	4	Pin	N	M, I	M	B, D
<i>Langloisia</i>	7	4	Pin	N	M, I	M	B, C
<i>Allophyllum</i>	9, 8	4	Pin	N	M	M	C
<i>Loeselia</i>	9	4	Pin	N, NW	M	M	C, D
<i>Leptodactylon</i>	9	4	Palm	N	M	M	D
<i>Linanthus</i>	9	4	Palm	N	M	M	D

† *Bonplandia geminiflora* chromosome number, $2n = 15$ bivalents, determined from the following collections: Sinaloa, Mexico, D. E. Breedlove 4463?; Chiapas, Mexico, D. E. Breedlove 56256. Vouchers deposited at CAS. Counted by A. Day.

sometimes merged 2–3 together. Diameter of bacula ca. 0.5 μ m. Reticulum supraverrucate. Verrucae on surface of exine very variable in shape and size, from very small and flat with diameter ca. 1 μ m to circular or oval with diameter to 10 μ m, in young pollen grains very densely spaced. Surface of verrucae ultra-finely striate or rugulate, as seen with scanning electron microscope at 7000 \times magnification.

This diagnosis is based on a single collection (Day and Moran 76133, CAS). Other collections show that the grains may be 7–8-colporate (Moran 7498, CAS) or the colpi may be longer (Fig. 6; Wiggins 5731, DS). Variation in the number and distribution of verrucae is seen by comparing Figures 5 and 6.

The most distinctive feature of *Acanthogilia* pollen grains is the coarsely verrucate exine (Fig. 5–8). Among other Polemoniaceae with zonocolporate grains, only *Eriastrum* and *Gilia* sect. *Giliastrum* have the exine verrucate, but there the verrucae are minute. Dr. Stuchlik (pers. comm. 1980) remarked that *Acanthogilia* has probably a new pollen type for the family.

Pollen grains with large verrucae do occur, however, in *Cantua*. In *C. buxifolia* Juss. ex Lam. (Fig. 9, 10) the exine appears much as in *Acanthogilia*. In both *C. buxifolia* and *Acanthogilia* the verrucae are diverse in size and shape, the larger ones supported by groups of bacula. Viewed with SEM (Fig. 9, 10), the verrucae of *C. buxifolia* differ from those of *Acanthogilia* only in being somewhat broader and flatter.

In the Cantueae (*Cantua* and *Huthia*) the exine is semitectate and, as illustrated (SEM) by Taylor and Levin (1975), generally consists of large, closely spaced areoles (Taylor and Levin's term) or insulae (Stuchlik 1967). However, *Cantua buxifolia* is exceptional in having areoles of such small diameter that they have been described as large verrucae (Erdtman 1952). This exine pattern may have evolved through reduction of larger areoles.

Despite the similarity in exine, the pollen grains of *Cantua buxifolia* differ from those of *Acanthogilia* in aperture type; for, as in other Cantueae, they are pantoporate, not zonocolporate. Since, however, both zonocolporate and pantoporate grains can occur within a single genus elsewhere (*Collomia*, Loeblich 1964, Chuang et al. 1978; *Gilia*, Stuchlik 1967), this difference between *Acanthogilia* and *Cantua* is not necessarily fundamental. In view of other notable shared

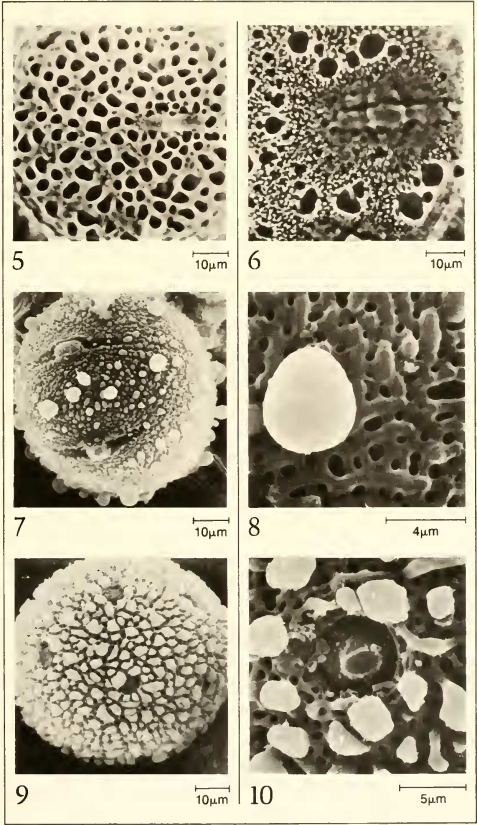
characters (Table 1), we interpret the similarity in exine as a mark of relationship.

On the basis of pollen morphology, Taylor and Levin (1975: fig. 1) grouped the genera of Polemoniaceae into four unnamed alliances (pollen groups 1–4 of our Table 1). One alliance included only *Cantua* and *Huthia*, but we would add *Acanthogilia*.

LEAVES.—In *Acanthogilia* the leaves of long shoots and axillary short shoots are markedly different, with no intermediates (Fig. 2F). The leaves of long shoots are woody-spinose and persistent, as in no other Polemoniaceae. Base and blade are scarcely delimited, and the blade is pinnately divided, with terete rachis and lobes. On the contrary, the fascicled axillary leaves are each clearly divided by a constriction into a persistent base and a deciduous blade (Fig. 11A). The broadened bases remain indefinitely in a compact spiral on the short shoot, but the blades fall at one time throughout the plant with drying of the season. These are smaller blades than those of the primary leaves, mostly simple, linear but flattened, herbaceous, and greener.

Cantua, *Huthia*, *Leptodactylon*, *Loeselia*, and some species of *Ipomopsis* also have leaves on long shoots and in axillary fascicles; but although the fascicled leaves may be smaller, all leaves are nearly alike. *Cantua* is somewhat exceptional: the primary leaves are large and more or less lobed and fall early, whereas the secondary, axillary leaves are more persistent and in most species are smaller and have entire margins (Infantes Vera 1962; Gibson 1967). In *C. buxifolia* grown in San Francisco, we note that, except for young shoots, leafy stems bear only the smaller secondary leaves. In various other Polemoniaceae, especially annuals, leaves are gradually different from base to apex, grading into bracts above. Only *Acanthogilia*, however, has markedly dimorphic leaves.

In most perennial Polemoniaceae the leaves wither persistent, though they may finally erode away. In several evergreen shrubs (*Cantua*, *Huthia*, *Loeselia mexicana* (Lam.) Brand, *L. purpusii* Brandegee), however, leaf blades finally fall, leaving the persistent bases conspicuous (Fig. 11B). In *Cantua buxifolia* and *C. pyrifolia* Juss. ex Lam., both of which produce fascicled leaves, the short shoots and crowded leaf bases, with blades gone, somewhat resemble those of *Acanthogilia* (Fig. 11A, B).



FIGURES 5-10. Pollen grains of *Acanthogilia gloriosa* and *Cantua buxifolia* Juss. ex Lam.; Fig. 5, 6. (light microscope) *Acanthogilia*; Fig. 5. Day and Moran 76-133 (CAS); Fig. 6. Wiggins 5731 (DS); Fig. 7, 8. (SEM) *Acanthogilia*, Wiggins 5731 (DS); Fig. 9, 10. (SEM) *Cantua buxifolia*, cultivated, McClintock s.n., 15 Mar 1976 (CAS).

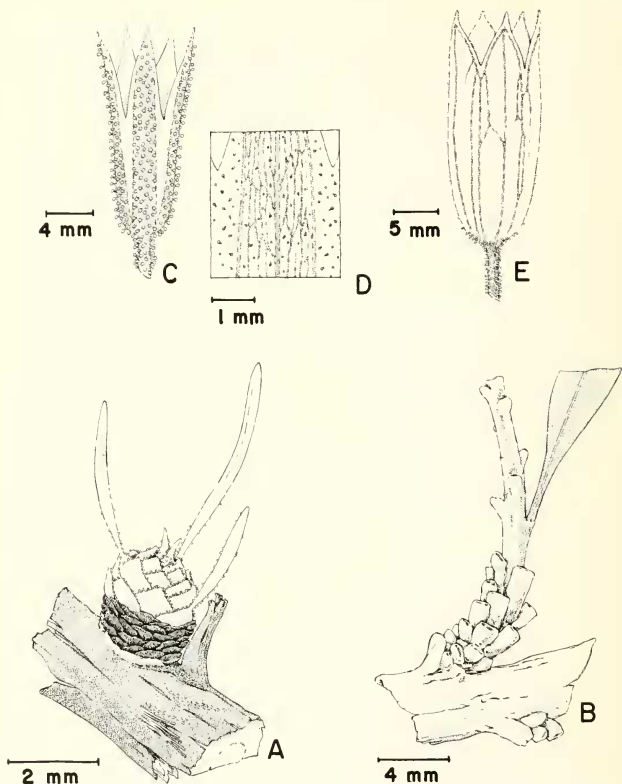


FIGURE 11. Short shoots and calyxes. A. Short shoot of *Acanthogilia gloriosa* with persistent leaf bases after most blades have fallen, the leaf bases from previous seasons compacted below, primary leaf mostly eroded away; B. Short shoot of *Cantua buxifolia* with crowded leaf bases, growing out into long shoot above; C. Calyx of *Acanthogilia gloriosa* at anthesis; D. Part of calyx, ventral side, showing venation in rib; E. Calyx of *Cantua buxifolia* at anthesis.

SEEDS. — The seed of *Acanthogilia* is flat and is bordered by a membranous wing 1–3 mm wide (Fig. 2C). In most Polemoniaceae, seeds are wingless, though in *Bonplandia* and *Loeselia* they

are sometimes very narrowly winged. Only in *Cantua*, *Cobaea*, and *Huthia* are the seeds likewise flat and broadly winged. In these genera, however, both seeds and wings are considerably

wider; and the wings, though thin, are opaque rather than membranous.

Acanthogilia has only 1–6 seeds per locule, whereas *Cantua*, *Cobaea*, and *Huthia* have many, in platelike layers. However, the ovary of *Acanthogilia* has 14–24 ovules per locule, suggesting that the ancestral capsule may have had many more seeds. A hint of layering in the capsules suggests that if more seeds were present they might form layers as in the other genera.

STAMENS.—The filaments of *Acanthogilia* are attached to the corolla tube about midway but are only superficially adnate below; they are well formed, with free margins, and are distinguishable to the base. Likewise in *Cobaea*, *Cantua* (*C. candelilla* Brand and *C. quercifolia* Juss. but not *C. buxifolia*), and *Gilia* sect. *Giliastrum* (*G. rigidula* Benth. and *G. ripleyi* Barneby but not *G. insignis* (Brand) Cory and Parks or *G. incisa* Benth.) the filaments are superficially adnate. This appears to be a rare and primitive condition in the family. In our sampling of other genera, the filaments are so merged with the corolla, at least basally and commonly to the point of insertion, that they are not distinguishable.

CALYX.—The calyx of *Acanthogilia* is narrowly membranous and veinless below the sinuses and has many veins crowded in the herbaceous ribs (Fig. 11C, D); it ruptures between ribs as the capsule grows. In eleven other genera (Table 1), including *Gilia* and most allies as well as *Phlox* and *Microsteris*, similarly, the calyx is narrowly to broadly membranous below the sinuses, with veins again confined to the ribs; it may or may not rupture in fruit. In all examples seen, veins are fewer and less crowded than in *Acanthogilia*. In all these genera, including *Acanthogilia*, lateral veins of adjacent ribs are connected only near the base of the calyx.

On the other hand, in *Booplandia*, *Cantua* (Fig. 11E), *Cobaea*, *Collomia*, *Gymnosteris*, *Huthia*, and *Polemonium* the calyx is not alternately ribbed and membranous but is herbaceous or somewhat chartaceous throughout, and it enlarges without rupturing as the capsule grows. Venation is various but generally is spread out more than in the genera with membranous calyx. Lateral veins of adjacent sectors may be connected just below the sinuses (Fig. 11E) or much lower. They are connected in *Cantua quercifolia* near the base of the calyx but in *C. buxifolia* at various levels, even in the same calyx (Fig. 11E).

The herbaceous calyx type, found also in related families, presumably is primitive in the Polemoniaceae, the membranous calyx perhaps arising independently in more than one line in arid habitats. A division of the family by calyx types then would separate some related genera. Thus *Collomia* (herbaceous calyx) belongs with the *Gilia* group (otherwise membranous), and *Phlox* and *Microsteris* (membranous calyx) seem related to genera with herbaceous calyx (Table 1). Similarly, *Acanthogilia* appears related to *Cantua* despite the difference in calyx (Table 1).

COROLLA VENATION.—Surveying corolla venation in the family, Day has found patterns to link *Acanthogilia* with some genera and to separate it from others. Generally in the family, each sector of the corolla has a median vein and two laterals more or less parallel in the tube, with branches in the lobes and commonly with connections; positions of vein connections are characteristic for many taxa. Figures 12–14 show examples from 12 out of 19 genera—all traced from photographs of dissected corollas stained with safranin. The staminal veins, alternating with the corolla veins in the tube, are omitted.

Venation patterns fall mainly into four types (identified in Table 1 by letters A–D): A. *Cantua* type—veins connected near corolla orifice, curving and connected once or twice above in the lobe (Fig. 12G–H, 13K–O); B. *Gilia* type—veins connected near orifice but straighter above and without other connections (Fig. 12B–D); C. *Loeselia* type—veins often connected near middle or apex of lobe but not near orifice (Fig. 14P–R); and D. *Leptodactylon* type—veins free, not connected in orifice or lobes, even in large corollas with many veins; often each sector with only a single vein in basal half of tube (Fig. 12E–F, 14S–U). Some genera show only one venation type, some two, and one three (Table 1). In very small corollas (*Microsteris*, Fig. 13J; many *Navarretia* species, Fig. 12A; *Gymnosteris*; and occasional species in other genera) venation may be so simplified that it tells little of relationship.

In *Acanthogilia* the corolla veins are connected at several levels in the lobes (Fig. 12H), much as in *Cantua*, *Cobaea*, and *Phlox* (Fig. 13). *Acanthogilia* differs from them in having more closely spaced veins that are nearly parallel and less curved. Its pattern is perhaps most closely ap-

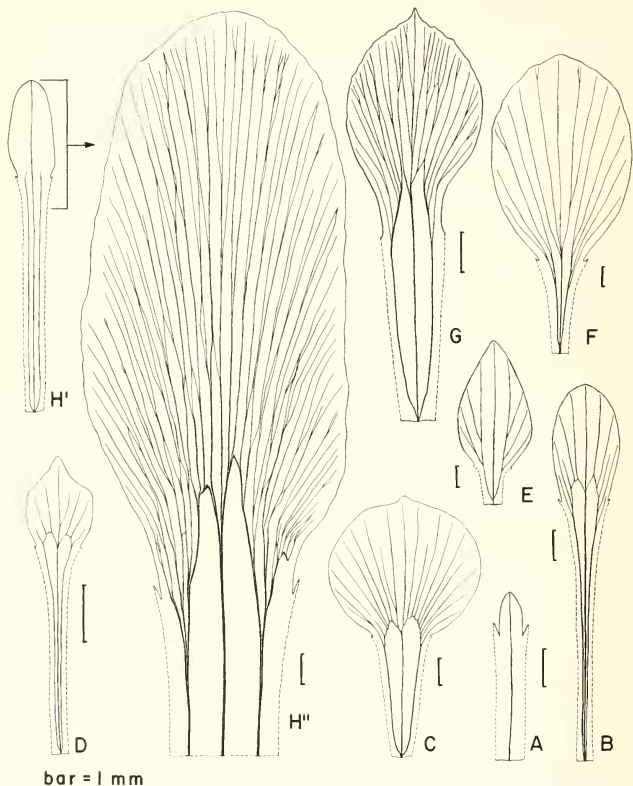
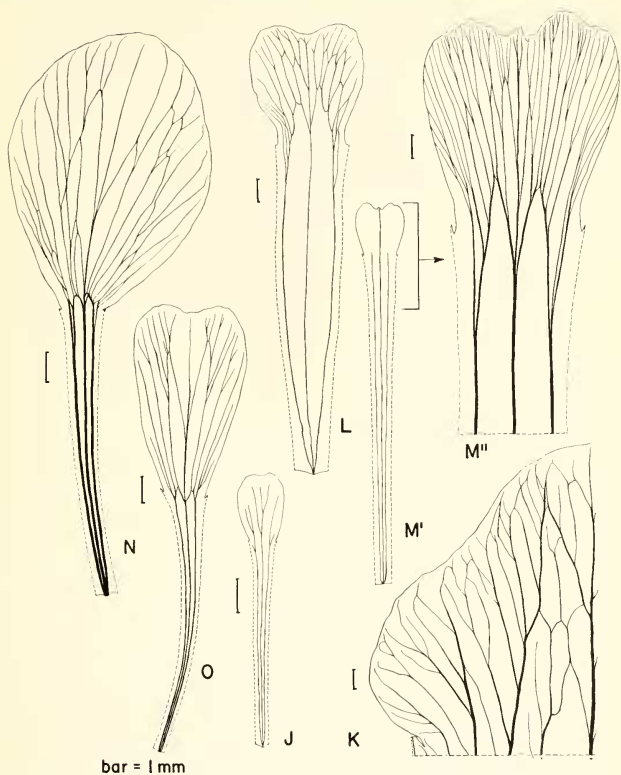


FIGURE 12. Corolla venation patterns in Polemoniaceae, each showing a sector from base of tube to apex of lobe. Dashed lines show where corolla tube cut. Stamens and staminal veins not shown. A. *Navarretia fossalis* Moran; B. *N. mitracarpa* Greene; C. *Gilia tricolor* Benth.; D. *G. leptomeria* Gray; E. *G. incisa* Benth.; F. *G. rigidula* Benth.; G. *G. ripleyi* Barneby; H', H". *Acanthogilia gloriosa* Day and Moran.

proached in *Cantua candelilla* (Fig. 13M). On the other hand, despite more numerous veins with connections at several levels, the pattern of *Acanthogilia* resembles that of *Gilia* and allies

(Fig. 12B-D) in its straighter and closer-spaced veins. And although most species of *Gilia* sect. *Giliastrum* have free veins (Fig. 12E-F), the anomalous *G. ripleyi* (Fig. 12G) has connections



bar = 1 mm

FIGURE 13. Corolla venation patterns, cont. J. *Microsteris gracilis* (Hook.) Greene; K. *Cobaea baurita* Standl.; L. *Cantua pyrifolia* Juss. ex Lam.; M', M'', *C. candelilla* Brand; N. *Phlox andicola* Nutt. ex Gray; O. *Bonplandia geminiflora* Cav.

at several levels, thus somewhat approaching *Acanthogilia*.

Although the species *gloriosa* has been placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, each of these genera has a venation pattern different from that of *Acanthogilia*. The distinc-

tive patterns of *Leptodactylon* and *Loeselia* especially seem to make close relationship with *Acanthogilia* unlikely.

WOOD ANATOMY.—Carlquist et al. (1984) studied the wood anatomy of the Polemoniaceae, comparing the relatively few woody species. Be-

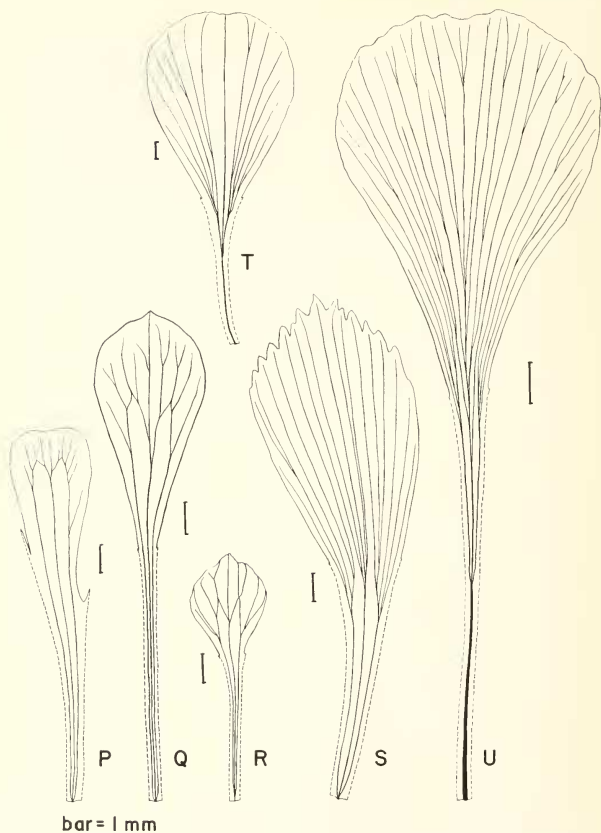


FIGURE 14. Corolla venation patterns, cont. P. *Loeselia greggii* S. Wats.; Q. *L. amplexens* (Hook. and Arn.) Benth.; R. *Allophyllum glutinosum* (Benth.) A. and V. Grant; S. *L. dianthiflorus* (Benth.) Greene; T. *L. grandiflorus* (Benth.) Greene; U. *Leptodactylon pungens* (Torr.) Rydb.

sides *Acanthogilia*, these species fall in *Cantua* and *Huthia* (Cantueae), *Cobaea* (Cobaeae), and *Eriastrum*, *Ipomopsis*, and *Leptodactylon* (Gilieae). In general, they thought the wood anatomy probably more closely correlated with growth form as related to habitat, than with systematic relationships.

The authors noted that *Acanthogilia* and a species of *Ipomopsis* are alike in having banded axile parenchyma—unusual in the family but occurring also, in its most incipient form, in *Cantua*. Likewise, in the imperforate tracheary elements and in the vascular rays, *Acanthogilia* is similar to *Ipomopsis* on the one hand and to the Cantueae on the other. The coincidence in these characters among *Acanthogilia*, the Gilieae, and the Cantueae somewhat parallels other similarities we report here (Table 1) and would seem to be due to relationships rather than to environmental factors alone.

RELATIONSHIPS

Acanthogilia is unique among Polemoniaceae in its extreme leaf dimorphism, its persistent woody-spinose primary leaves, and its coarsely verrucate zonocolporate pollen grains. Although *A. gloriosa*, the sole species, has been placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, it differs further from all these genera in its persistent secondary leaf bases with deciduous blades, its numerous closely spaced corolla veins with interconnections at several levels, and its winged seeds, and from all these except for two species of *Gilia* in its superficially adnate filaments. It differs still further from *Gilia* and *Ipomopsis* in its large shrubby habit, from *Ipomopsis* in its basic chromosome number of nine, and from *Leptodactylon* in its pinnate leaves and its three corolla veins instead of one in each sector of the lower tube.

Among North American Polemoniaceae, *Acanthogilia* seems to have most in common with *Gilia* and allies, and especially with species of *Gilia* sect. *Giliastrum*. As in *Acanthogilia*, all *Gilia* species have the calyx membranous below the sinuses, and most, including sect. *Giliastrum*, have zonocolporate pollen and have the primitive $x = 9$. In this polymorphic genus of five sections, usually the pollen is blue and the exine reticulate to striate and not verrucate. In sect. *Giliastrum*, however, the pollen is yellow as in *Acanthogilia*, and the exine is somewhat similar,

being peritectate and minutely verrucate whereas in *Acanthogilia* it is perreticulate and coarsely verrucate. Although in most species of *Gilia* the filaments merge with the corolla below, in *G. ripleyi* and *G. rigidula*, of sect. *Giliastrum*, the filaments are superficially adnate, as in *Acanthogilia*. Most species of *Gilia* are annual and none are truly woody, but *G. ripleyi* is a suffrutescent perennial. Finally, although most species of sect. *Giliastrum* have free corolla veins, *G. ripleyi* is unique in *Gilia* and further resembles *Acanthogilia* in having the veins connected at several levels.

Acanthogilia is perhaps most closely related to the Andean genus *Cantua*. *Cantua*, like *Acanthogilia*, is shrubby, with leaves dimorphic, borne on long shoots and axillary short shoots, with crowded leaf bases remaining on the short shoots after the blades have fallen, with corolla veins connected at more than one level, with seeds flattened and broadly winged, with a basic chromosome number of nine, with superficially adnate filaments in *C. candelilla* and *C. quercifolia*, and with coarsely verrucate pollen in *C. buxifolia*. The lower branches of *C. buxifolia* (grown in San Francisco) take root, as do those of *Acanthogilia*. *Cantua* differs in that the leaves are broadly herbaceous and only slightly dimorphic, with primary leaves deciduous, not at all woody-persistent, and secondary leaves more persistent; the calyx herbaceous, not membranous below the sinuses, and not rupturing in age; the pollen pantoporate, not zonocolporate; the chromosome number hexaploid, not diploid. We suggest that *Acanthogilia* may be a specialized desert descendent of a diploid line also ancestral to *Cantua*. Since *Cantua* is hexaploid, however, and probably amphiploid, such divergent characters as the herbaceous calyx may perhaps derive from some other line.

Grant (1959) divided the Polemoniaceae into five tribes. *Acanthogilia* probably belongs to the Cantueae but apparently has some relationship also with the Gilieae. Much new evidence bearing on generic relationships has accumulated, especially from pollen studies, since Grant's classification, and the time seems ripe for a new tribal arrangement.

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